

Game Theory in Biology

Concepts and Frontiers

JOHN M. McNAMARA

School of Mathematics, University of Bristol, UK

OLOF LEIMAR

Department of Zoology, Stockholm University, Sweden

OXFORD
UNIVERSITY PRESS

Contents

Acknowledgements	xi
1 Setting the Scene	1
1.1 Introduction	1
1.2 Frequency Dependence	2
1.3 The Modelling Approach	6
1.4 Scope of the Field and Challenges	7
1.5 Approach in This Book	9
2 Central Concepts	13
2.1 Actions, States, and Strategies	13
2.2 The Phenotypic Gambit	16
2.3 Invasion Fitness	19
2.4 Evolutionary Endpoints	22
2.5 Fitness Proxies	23
2.6 From Strategies to Individuals	25
3 Standard Examples	27
3.1 Contributing to the Common Benefit at a Cost	27
3.2 Helping Others: The Prisoner's Dilemma Game	30
3.3 The Tragedy of the Commons	31
3.4 Biparental Care: The Parental Effort Game	32
3.5 Contest Over a Resource: The Hawk–Dove Game	36
3.6 The Evolution of Signalling: From Cue to Signal	41
3.7 Coordination Games	44
3.8 Produce Sons or Daughters? The Sex-Allocation Game	45
3.9 Playing the Field	48
3.10 Dispersal as a Means of Reducing Kin Competition	48
3.11 Threshold Decisions	50
3.12 Assessment and Bayesian Updating	56
3.13 Exercises	60

4	Stability Concepts: Beyond Nash Equilibria	63
4.1	Evolutionarily Stable Strategies	64
4.2	Adaptive Dynamics	69
4.3	Evolution to a Fitness Minimum	74
4.4	Replicator Dynamics	79
4.5	Games Between Relatives	81
4.6	Exercises	87
5	Learning in Large Worlds	91
5.1	Reinforcement Learning	92
5.2	Learning and the Hawk–Dove Game	96
5.3	Learning in a Game of Joint Benefit of Investment	99
5.4	A Dominance Game	102
5.5	Approaches to Learning in Game Theory	107
5.6	Exercises	109
6	Co-evolution of Traits	111
6.1	Stability in More than One Dimension	112
6.2	Role Asymmetries	114
6.3	The Evolution of Anisogamy	118
6.4	Evolution of Abilities and Role Specialization	122
6.5	Learning and Individual Specialization	126
6.6	Co-evolution of Prosociality and Dispersal	130
6.7	Co-evolution of Species	133
6.8	Concluding Comments	137
6.9	Exercises	138
7	Variation, Consistency, and Reputation	141
7.1	Variation has Consequences	141
7.2	Variation and the Stability of Equilibria	143
7.3	Taking a Chance	145
7.4	Signalling and the Handicap Principle	148
7.5	Reputation	150
7.6	Indirect Reciprocity	153
7.7	Differences Select for Social Sensitivity	157
7.8	Markets	160
7.9	Choosiness, Assortment, and Cooperation	164
7.10	Commitment	166
7.11	Exercises	169
8	Interaction, Negotiation, and Learning	173
8.1	Interaction over Time	173
8.2	Information and the Order of Choice	174

8.3	Credible Threats and Strategic Commitment	177
8.4	Negotiation between Partners	180
8.5	Evolution of Cognitive Bias	185
8.6	Social Dominance	188
8.7	Assessment in Contests	193
8.8	Outlook: Games with Interaction over Time	198
8.9	Exercises	201
9	Games Embedded in Life	203
9.1	Self-consistency	203
9.2	The Shadow of the Future, and the Past	204
9.3	Resident Strategy Affects Future Opportunities	206
9.4	Dependence on Future Actions	209
9.5	Territorial Defence and the Desperado Effect	216
9.6	State-dependent Ideal Free Distributions	221
9.7	Is it Worth it?	226
9.8	Exercises	228
10	Structured Populations and Games over Generations	231
10.1	Invasion Fitness for Structured Populations	233
10.2	Offspring Quality versus Number	236
10.3	Reproductive Value Maximization	240
10.4	Sex Allocation as a Game over Generations	242
10.5	The Fisher Runaway Process	246
10.6	Maximizing Lifetime Reproductive Success	252
10.7	Dispersal	255
10.8	Evolutionary Analysis in Structured Populations	257
10.9	Exercises	258
11	Future Perspectives	261
11.1	Phylogeny	263
11.2	Behavioural Mechanisms in Large Worlds	266
11.3	Ontogeny and the Acquisition of Behaviour	271
	Appendix A: Summary of Notation	273
	Appendix B: Solutions to Exercises	275
	References	305
	Index	325